Reference: *Biol. Bull.* **187:** 304–308. (December, 1994)

# Temperature and the Larval Ecology of the Crown-of-Thorns Starfish, *Acanthaster planci*

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*The recently reported dramatic population increases (outbreaks) of the coral-eating crown-of-thorns starfish,* Acanthaster planci, *which have damaged many reefs in the Indo-Pacific, are ending (1), but questions remain about the factors that affect* Acanthaster *distribution and densities. For example, the narrow temperature tolerance (26° or 27° to 30° or 31°C) reported for* Acanthaster's *larval development (2) is problematic because* Acanthaster *occurs where temperatures do not rise into this range (3, 4). We have further examined some temperature relationships in* Acanthaster's *early development. Cleavage proceeded normally over a range of about 10°C, but specific limiting temperatures depended upon the geographic source of the parents or their recent history of temperature exposure. Hatched, swimming gastrulae continued normal development to bipinnaria throughout a temperature range of 13°C. These results indicate that the narrow developmental temperature tolerances reported earlier for* Acanthaster *do not apply to all early developmental stages, and they add to the list of larval adaptations that can facilitate dispersal of* Acanthaster *larvae and propagation of outbreaks.*

*Acanthaster planci* is one of several Indo-Pacific asteroids that prey on coral polyps (5). Unlike other tropical starfish, however, *Acanthaster* undergoes occasional population outbreaks that have severely reduced coral cover on many reefs over the last 30 years. The causes of these outbreaks remain obscure despite much recent research (6–8). The outbreaks may be natural phenomena with a long history of occurrence (9), or they may be relatively recent in origin, brought about as a result of human activities (10). A combination of both explanations is also possible (11).

Two series of outbreaks of *Acanthaster planci* have been recorded on Australia's Great Barrier Reef (GBR) since the early 1960s, affecting reefs over approximately the central third of that system (12). Kenchington (13) hypothesized that outbreaks (termed primary) began somewhere to the north of Green Island (Fig. 1), and in turn initiated a cascade of additional outbreaks (termed secondary) that spread southward as a result of the advection of larvae by southward-flowing currents during the spawning season. Recent data from broadscale population surveys (1), genetic studies (14), and hydrodynamic models (15, 16) support Kenchington's hypothesis, though questions have been raised regarding some hydrodynamic models (17).

Population outbreaks of *Acanthaster* on the GBR have occurred over some 1000 km of reef (6 degrees of latitude). The main wave of outbreaks declined at around 20° S (18), which lies to the south of Davies Reef (Fig. 1); only a few smaller outbreaks are now being recorded at the far southern end of the system in the Swain complex (1). Lucas (2) has hypothesized that southern limits of *Acanthaster's* distribution may be dictated by larval temperature requirements. However, *Acanthaster* occurs in cooler waters near the limits of hard coral distribution (3, 4, 7). Temporally variable aggregations of *Acanthaster* at some Japanese sites appear to be derived entirely from settlement of larvae carried by currents from warmer water areas (19), but at other cooler water sites there are relatively stable *Acanthaster* populations. For example, there is evidence of increasing *Acanthaster* numbers at Lord Howe Island (Fig. 1) (20), although the mean surface water temperature there during January, the warmest month of the year, is about 24°C, which is below the reported range of developmental temperature tolerance. Population maintenance there conceivably could depend solely upon recruitment of larvae carried by currents from the GBR,

Received 3 January 1994; accepted 3 October 1994.

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**Figure 1.** Map showing collection sites and other locations mentioned in the text.

but the Lord Howe Island population is genetically divergent from GBR populations (21), and gene flow into it from the GBR appears to be very limited, indicating a relatively isolated, locally reproducing population. Such evidence of successful reproduction under diverse environmental temperature regimes and genetic evidence for long-distance larval transport (14) suggest complexity in *Acanthaster's* developmental temperature relationships. We have investigated both the developmental temperature tolerances of offspring of geographically widely separated groups of *Acanthaster* and the effects of experimentally altering temperature exposures of adult, embryonic, and larval starfish.

Offspring of animals collected off the Gove Peninsula near Nhulunbuy and at Davies Reef in the GBR (Fig. 1) completed development to bipinnaria larvae equally well at 31°, 27°, and 24°C. At 22.3° and 21°C, Davies Reef embryos produced normal bipinnariae (Table I). At the same temperatures, some Gove embryos hatched, but they ceased development as abnormal early gastrulae.

Such geographic differences in developmental temperature tolerance may be due to genetic differentiation of separated populations, physiological acclimatization effects reflecting recent parental temperature exposure, or a combination of the two (22–24). We conducted a laboratory acclimation experiment to investigate a possible parental acclimatization effect in *Acanthaster.* A group of adults from Davies Reef was separated into two samples. One sample was held for 18 days at 31°C and the other at 25°C for 21 days. We observed differences between the offspring of 25°-acclimated animals and 31°-acclimated animals in tolerance to lower temperatures (Table I) and in early cleavage rates (Fig. 2), which in other echinoderms are proportional to overall developmental rates at least to the gastrula stage (25). The tolerance difference indicates an acclimatory translation of tolerance range, but more data at several temperatures would be needed to determine if the observed rate difference resulted from rotation of the rate: temperature curve.

We also examined possible parental effects due to seasonal change in water temperature in animals studied immediately after collection at Davies Reef in October (temperature at collection site: 25.5°C) and in November (temperature: 27°C). Offspring of the two groups differed in their tolerance to high temperature. In October-collected animals, development to early bipinnaria larvae proceeded normally between 21° and 27°C, but not at 32°C. However, offspring of November-collected animals developed into normal bipinnaria at 32°. This seasonal change resembles those reported for other echinoderms (26, 27).

Thus early developmental temperature tolerances in *Acanthaster* vary with recent parental temperature exposure as well as geographic source. However, our results do not distinguish the relative contributions made by

**Table I**

*Development of embryos from each of four groups at low experimental temperatures*

| Group | Zygote to Bipinn. @ 22.3°C | Zygote to Bipinn. @ 21°C | Cleavage @ 18°C |
|---|---|---|---|
| DAVIES | + | + | none |
| GOVE | — | — | none |
| 31°-ACCL | — | — | none |
| 25°-ACCL | + | ◇ | abnormal |

Bipinn. = bipinnaria larva; + indicates normal development to bipinnaria larvae; — indicates failure to develop to bipinnariae; ◇ indicates development of larvae with clumps of extra mesenchyme-like cells rarely observed in embryos developing at 31°, 27°, or 24°C. Gamete shedding was induced by 1-methyl adenine injection. Zygotes were transferred to rearing dishes at experimental temperatures within 5 min after fertilization at room temperature (24°C). Animals were collected off Nhulunbuy on the Gove Peninsula and at Davies Reef on 18 and 19 December 1991, and maintained in running seawater at approximately 27° until experiments began early in January 1992. Acclimation of samples of Davies Reef animals began on 3 January 1992, and continued at 31°C for 18 days and at 25°C for 21 days.

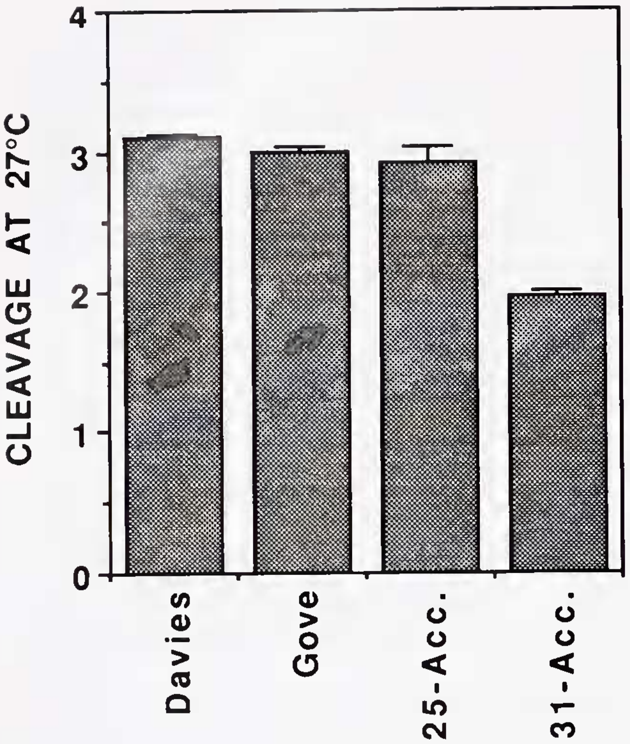

**Figure 2.** Cleavage rate comparisons at 27°C. For each group, four replicate cultures in 20-ml scintillation vials (mean no. of embryos per vial = 99) were fixed after 146 min. Embryos in each culture were counted and scored for cleavages completed. Bars represent means of individual culture means, with standard errors. Because ANOVA indicated a significant treatment effect, the Tukey test was applied. The mean for the 31°- acclimated group differs significantly from the other means ($\alpha = 0.05$), which do not differ from one another.

population genetic differentiation and physiological acclimatization to the observed geographic variations.

Because of its importance for dispersal, the temperature tolerance of newly hatched swimming embryos was examined. Early gastrulae from cultures of Gove embryos were transferred to 21° and 18°C (temperatures at which Gove embryos cannot cleave normally). Transferred embryos continued to swim, completed gastrulation, and produced bipinnariae at both temperatures (Table II). This unexpectedly broad temperature tolerance in gastrula-stage embryos prompted additional transfer experiments. Newly hatched Davies Reef gastrulae transferred from 27° to 18.5°C developed into bipinnariae that appeared normal (Fig. 3). Even gastrulae transferred from 27° to 15°C and held there for 6 days continued to swim actively, slowly continued archenteron extension, and then quickly completed bipinnaria morphogenesis after transfer back to 27°C. However, these larvae contained clumps of extra mesenchyme-like cells.

Table II

*Results of gastrula transfer experiments with Gove embryos*

| Transfer group | Days | Percent Bipinn. development |
|---|---|---|
| 31° to 31° (Control) | 2 | 93 |
| 31° to 21° | 5 | 88 |
| 31° to 18° | 17 | 81 |

Only swimming, newly hatched, early gastrulae were transferred. The numbers of days from transfer to final observation are given. Comparable results were obtained following transfers of embryos that developed from fertilization to hatching at 27°C.

In summary, data presented here support a modified concept of temperature tolerance during early *Acanthaster* development (Fig. 4), indicating that *Acanthaster's* distribution and abundance need not be as limited by developmental temperature as previously thought. Clearly, temperature relationships in later larval stages should be

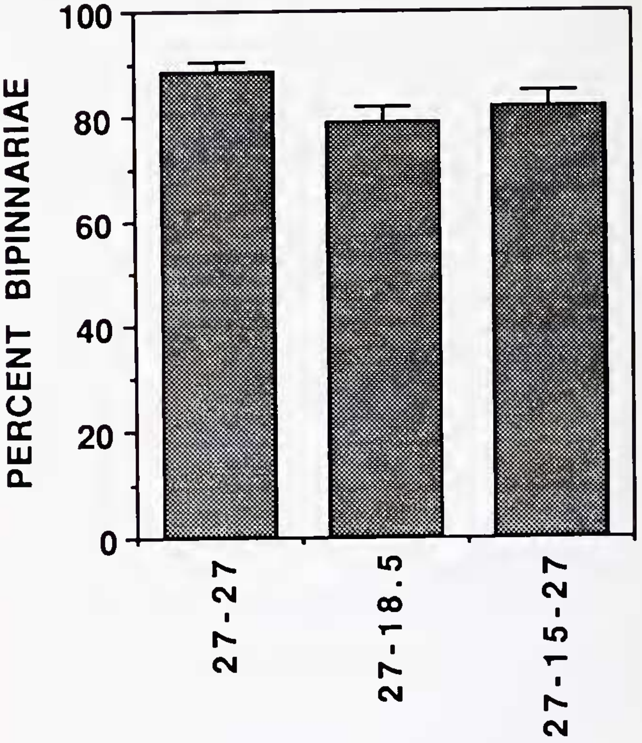

**Figure 3.** Gastrula transfer experiments with Davies Reef animals during December 1992. Early development proceeded at 27°C, and transfers were as described in Table II. Bars represent mean percentages, with standard errors, of bipinnaria development for 12 cultures (40 to 100 embryos in each) from two experiments. "27–27" represents controls; "27–18.5" represents transfer and continuing development at 18.5°C; and "27–15-27" represents gastrulae returned to 27°C after 6 days at 15°C. Bipinnariae in this latter group were normal in shape, but many contained clumps of extra mesenchyme-like cells. Embryos that were not returned from 15° to 27°C showed some archenteron extension, but eventually regressed and died.

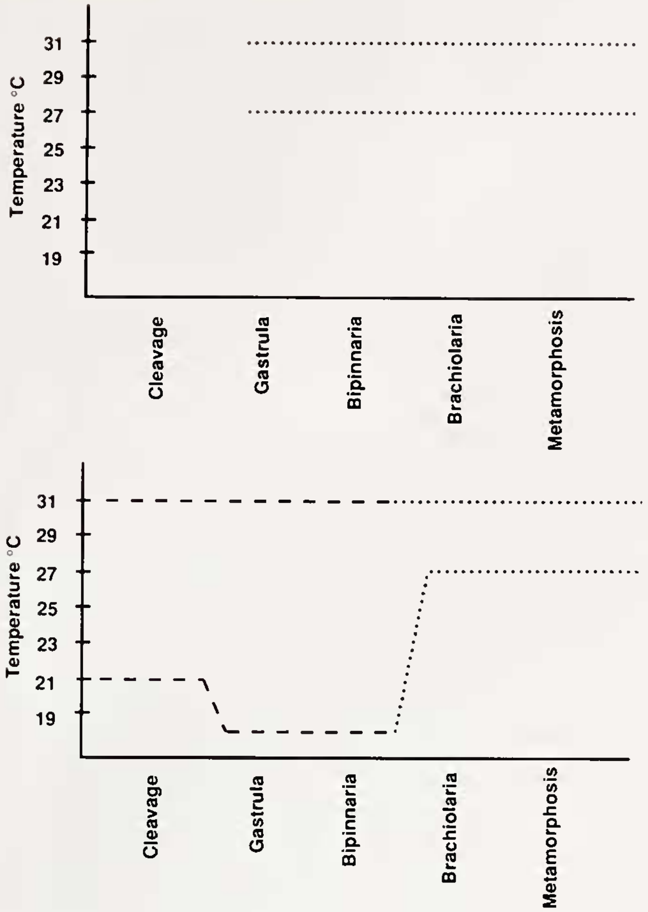

**Figure 4.** Conceptual models of crown-of-thorns starfish developmental temperature tolerances. The upper model is one inferred from data of Lucas (2) who transferred embryos at hatching and maintained cultures until settling and metamorphosis. The lower model retains the limited temperature tolerances (dotted lines) reported by Lucas for later larval stages, but incorporates the broader tolerances (dashed lines) of earlier developmental stages indicated by our data. Our data also indicate that actual limiting temperatures, but not necessarily size, of tolerance ranges vary with recent parental temperature exposure as well as geographic source.

reexamined, especially for populations at the extremes of *Acanthaster's* distribution. Further, the temperature tolerance of *Acanthaster* gastrulae adds to a list of traits that make *Acanthaster* larvae particularly well adapted for long-distance dispersal. Even larvae swept into cooler water could very slowly continue normal development during transport. This, along with the ability to develop at the low phytoplankton concentrations common in tropical waters (28, 29) and the negatively geotropic swimming behavior characteristic of *Acanthaster* gastrula (3), would allow transport to distant reef sites with conditions appropriate for later larval development and settling—processes that may be less resistant to environmental variation (2). Early larval hardiness may facilitate both the routine dispersal of larvae and the propagation of *Acanthaster* outbreaks.

## Acknowledgments

This work was funded by the Great Barrier Reef Marine Park Authority through the Crown-of-Thorns Starfish Research Committee. We thank C. Cartwright, K. Hall, and D. Whitehead for technical assistance, P. Moran and C. Mundy for discussion and advice, J. Quam for map preparation, and C. Christie for collecting *Acanthaster* at Nhulunbuy.

## Literature Cited

1. **Moran, P. J., G. De'ath, V. J. Baker, D. K. Bass, C. A. Christie, I. R. Miller, B. A. Miller-Smith, and A. A. Thompson. 1992.** Pattern of outbreaks of crown-of-thorns starfish (*Acanthaster planci* L.) along the Great Barrier reef. Pp. 555–568 in *Crown-of-Thorns Starfish on the Great Barrier Reef: Reproduction, Recruitment and Hydrodynamics*, C. Johnson, ed. *Aust. J. Mar. Freshwater Res.* **43(3).**
2. **Lucas, J. S. 1973.** Reproductive and larval biology of *Acanthaster planci* in great Barrier Reef waters. *Micronesica* **9:** 197–203.
3. **Yamaguchi, M. 1973.** Early life histories of coral reef asteroids, with special reference to *Acanthaster planci* (L.). Pp. 369–387 in *Biology and Geology of Coral Reefs, Vol. 2,* O. A. Jones and R. Endean, eds. Academic Press, New York.
4. **McKnight, D. G. 1978.** *Acanthaster planci* (Linnaeus) (Asteroidea: Echinodermata) at the Kermedec Islands. *N. Z. Oceanogr. Inst. Rec.* **4:** 17–19.
5. **Birkeland, C. 1989.** The influence of echinoderms on coral-reef communities. Pp. 1–79 in *Echinoderm Studies, Vol. 3,* M. Jangoux and J. M. Lawrence, eds. A. A. Balkema, Rotterdam.
6. **Zann, L. P., and P. J. Moran. 1988.** A coordinated research program on the *Acanthaster* phenomenon. Pp. 177–182 in *Proc. Sixth Int. Coral Reef Symp. Vol. 2.*
7. **Birkeland, C. and J. S. Lucas. 1990.** *Acanthaster planci: Major Management Problem of Coral Reefs.* CRC Press, Boca Raton, FL.
8. **Johnson, C., ed. 1992.** *Crown-of-Thorns Starfish on the Great Barrier Reef: Reproduction, Recruitment and Hydrodynamics. Aust. J. Mar. Freshwater Res.* **43(3).**
9. **Walbran, P. D., R. A. Henderson, A. J. T. Jull, and M. J. Head. 1989.** Evidence from sediments of long-term *Acanthaster planci* predation on corals of the Great Barrier reef. *Science* **245:** 847–850.
10. **Cameron, A. M., R. Endean, and L. M. DeVantier. 1991.** Predation on massive corals: Are devastating population outbreaks of *Acanthaster planci* novel events? *Mar. Ecol. Prog. Ser.* **75:** 251–258.
11. **Moran, P. J., and R. H. Bradbury. 1989.** The crown-of-thorns starfish controversy. *Search* **20:** 3–6.
12. **Reichelt, R. E., R. H. Bradbury, and P. J. Moran. 1990.** Distribution of *Acanthaster planci* outbreaks on the Great Barrier Reef between 1966 and 1989. *Coral Reefs* **9:** 97–103.
13. **Kenchington, R. A. 1977.** Growth and recruitment of *Acanthaster planci* (L.) on the Great Barrier Reef. *Biol. Conservation* **11:** 103–118.
14. **Benzie, J. A. H., and J. A. Stoddart. 1992.** Genetic structure of outbreaking and non-outbreaking crown-of-thorns starfish (*Acanthaster planci*) populations on the Great Barrier Reef. *Mar. Biol.* **112:** 119–130.
15. **James, M. K., and J. P. Scandol. 1992.** Larval dispersal simulations: correlation with the crown-of-thorns starfish outbreaks database. Pp. 569–582 in *Crown-of-Thorns Starfish on the Great Barrier Reef:*

*Reproduction, Recruitment and Hydrodynamics.* C. Johnson, ed. *Aust. J. Mar. Freshwater Res.* **43(3).**

16. **Scandol, J. P., and M. K. James. 1992.** Hydrodynamics and larval dispersal: a population model of *Acanthaster planci* on the Great Barrier Reef. Pp. 583–596 in *Crown-of-Thorns Starfish on the Great Barrier Reef: Reproduction, Recruitment and Hydrodynamics.* C. Johnson, ed. *Aust. J. Mar. Freshwater Res.* **43(3).**
17. **Wolanski, E. 1993.** Facts and numerical artefacts in modelling the dispersal of crown-of-thorns starfish larvae in the Great Barrier Reef. *Aust. J. Mar. Freshwater Res.* **44:** 427–436.
18. **Moran, P. J. 1986.** The *Acanthaster* phenomenon. *Oceanogr. Mar. Biol. Annu. Rev.* **24:** 379–480.
19. **Yamaguchi, M. 1987.** Occurrences and persistency of *Acanthaster planci* pseudo-population in relation to oceanographic conditions along the Pacific coast of Japan. *Galaxea* **6:** 277–288.
20. **DeVantier, L. M., and G. Deacon. 1990.** Distribution of *Acanthaster planci* at Lord Howe Island, the southern-most Indo-Pacific reef. *Coral Reefs* **9:** 145–148.
21. **Benzie, J. A. H., and J. A. Stoddart. 1992.** Genetic structure of crown-of-thorns starfish (*Acanthaster planci*) in Australia. *Mar. Biol.* **112:** 631–639.
22. **Moore, J. A. 1949.** Geographaphic variation of adaptive characters in *Rana pipiens* Schreber. *Evolution* **3:** 1–24.
23. **Tester, P. A. 1985.** Effects of parental acclimation temperature and egg-incubation temperature on egg-hatching time in *Acartia tonsa* (Copepoda: Calanoida). *Mar. Biol.* **89:** 45–53.
24. **Johnson, L. G. 1993.** Temperature tolerance, temperature stress, and animal development. Pp. 37–40 in *Proceedings of the Biostress Symposia.* N. H. Granholm, ed. South Dakota State Univ., Brookings.
25. **Fujisawa, H. 1989.** Differences in temperature dependence of early development of sea urchins with different growing seasons. *Biol. Bull.* **176:** 96–102.
26. **O'Connor, C., and J. C. Mulley. 1977.** Temperature effects on periodicity and embryology, with observations on the population genetics, of the aquacultural echinoid *Heliocidaris tuberculata.* *Aquaculture* **12:** 99–114.
27. **Horstadius, S. 1975.** A note on the effect of temperature on sea urchin eggs. *Exp. Mar. Biol. Ecol.* **18:** 239–242.
28. **Olson, R. R. 1987.** *In situ* culturing as a test of the larval starvation hypothesis for the crown-of-thorns starfish, *Acanthaster planci.* *Limnol. Oceanogr.* **32:** 895–904.
29. **Ayukai, T. 1994.** Ingestion of ultraplankton by the planktonic larvae of the crown-of-thorns starfish, *Acanthaster planci.* *Biol. Bull.* **186:** 90–100.